

AN EMBRYOLOGICAL ANALYSIS OF MYRTALES: ITS DEFINITION AND CHARACTERISTICS¹

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ABSTRACT

A combination of embryological characteristics clearly defines Myrtales as comprising Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae, a circumscription that agrees with that of the "core" Myrtales given by Dahlgren and Thorne (1983). The ordinal characteristics are: 1) anther tapetum glandular, 2) ovule crassinucellate, 3) inner integument 2-layered (except in *Syzygium*), 4) micropyle formed by both integuments (except in *Syzygium* and *Trapa*), 5) antipodal cells ephemeral or absent, 6) endosperm formation Nuclear type and 7) seed exalbuminous. Haloragaceae, Lecythidaceae, and Thymelaeaceae definitely should be excluded from Myrtales on the basis of differences in three or more of these primary defining characteristics. On the other hand, embryological evidence does not contradict the possibility of a relatively close relationship between Elatinaceae and Myrtales, even though an overall consideration of their features seems to make such a relationship seem less likely. Embryological evidence indicates a considerable degree of heterogeneity in Rhizophoraceae, a family or group of families that is clearly not assignable to Myrtales.

INTRODUCTION

Although embryology has been an important source of evidence for the relationships of angiosperms for more than a century, both the tedious nature of the processes needed to prepare materials for embryological study and the difficulty of obtaining samples of key genera have retarded progress in this area. During the course of the past 50 years several authors including Schnarf (1931), Maheshwari (1950), and Davis (1966) have compiled the accumulated data on the embryology of angiosperms, and their books have been of use as guides to the literature. A number of other authors, including Maheshwari (1964), Davis (1966), Brewbaker (1967), and Philipson (1974), have evaluated the significance of individual characters or assemblages of characters in considering the relationships of different groups of angiosperms. In 1967, a symposium on the comparative embryology of angiosperms was held in India, including discussions of the positions of several critical families. Taken together, this literature has supported the view that embryological characteristics have a great deal to offer as sources of evidence for the systematics of higher-level groups among the flowering plants.

In this paper, we have analyzed the available information concerning the embryology of Myr-

tales and a few other families that have been thought to be closely related to this order. Our primary purpose has been to characterize Myrtales embryologically and to chart the main outlines of relationship within the order from an embryological perspective. As defined by Dahlgren and Thorne (1983), the families of core Myrtales are: Combretaceae, Crypteroniaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae. In addition, Chrysobalanaceae, Coridaceae, Elaeagnaceae, Elatinaceae, Haloragaceae, Lecythidaceae, Rhizophoraceae, Thymelaeaceae, which are excluded from the order by Dahlgren and Thorne (1983) but are "in various respects conspicuously similar to Myrtales," are analyzed from an embryological point of view in the light of the available information. We offer the present critical review to bring together all available literature and to serve as a guide to the most appropriate directions for future studies of the embryology of Myrtales.

METHODS

In the course of this review we have analyzed nearly all of the references cited by Davis (1966), as well as the subsequent publications that have

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been available to us. Not all of these publications included information that was valuable for evaluating the embryology of Myrtales, and many had incomplete or inadequate information. For example, since the work of Geerts (1908) it has been understood that Onagraceae have the distinctive *Oenothera*-type embryo sac development. Earlier references such as those of Hofmeister (1847, 1858), Vesque (1879a, 1879b), Ward (1880), and Guignard (1882) were not able to explain this type of embryo sac development fully owing to the less precise techniques used in the nineteenth century (Maheshwari, 1948). Similarly, most other nineteenth-century embryological studies have relatively little to offer for current evaluations of the relationships of the families of angiosperms.

In general, only representative genera from individual families have been examined. The power of our comparisons between families is derived from the depth and scope of earlier investigations. We have attempted to take this factor into account in utilizing and evaluating the published information about the embryology of Myrtales and allied groups as follows:

$$\text{Level of knowledge (\%)} = \frac{\text{Total number of embryological studies of anthers, ovules, and seeds of genera of a given family}}{3 \times (\text{number of genera of the family})} \times 100$$

We have divided the embryological data reviewed into three parts: namely, that concerning the anthers, ovules, and seed development. Most of the references we consulted refer to only one or two of these three major components of embryology. Comprehensive studies of all three classes of data provide the only sound basis for evaluating the relationships of genera and families. Even if some information is available, it may be strictly limited, and may therefore be of relatively little use. It is very rare, for example, for an earlier study to describe accurately the thickness of the integuments.

A second problem in utilizing published data concerning embryology concerns nomenclature. Names have sometimes changed so often in the past that it is difficult to be certain how many taxa are involved among those studied earlier. Except for Onagraceae and Penaeaceae, we have in general accepted the nomenclature used in the

articles involved as a basic guide to the number of taxa studied earlier. For the number of genera in a given family, we have used Cronquist (1981) as a reference.

Despite these difficulties, we hope that our evaluation of the amount of knowledge available concerning the embryology of particular families will be useful in arriving at a sound understanding of the thoroughness of the earlier studies of the group and thus help the usefulness of the conclusions drawn for an evaluation of relationships.

EMBRYOLOGICAL CHARACTERS USED FOR ANALYSIS

The characters that are treated as most important in making these evaluations are basically those that Maheshwari (1964), Davis (1966), and Palser (1975) have considered "embryological characters of taxonomic significance." We have elected to use the whole set of characteristics so as to make what we believe to be the most effective comparison between families. Consequently, we have added several characters, such as thickness of integuments and presence or absence of fatty globules in megaspores of embryo sacs, to those treated as fundamental by the authors just mentioned. Specifically, we have dealt with the following 35 characters:

Anthers:

1. Number of sporangia per anther: four or more.
2. Type of wall development: Basic, Dicotyledonous, Monocotyledonous, Reduced.
3. Epidermis: persistent or not.
4. Endothecium develops fibrous thickenings or not.
5. Middle layers: persistent or not.
6. Tapetum: glandular or amoeboid.
7. Number of nuclei in a tapetal cell: one, two, or more.
8. Cytokinesis in a microspore mother cell: simultaneous or successive.
9. Shape of microspore tetrads: tetrahedral, decussate, isobilateral, or otherwise.
10. Number of cells in a mature pollen: one or two.

Ovules:

11. Degree of ovule curvature: anatropous, campylotropous, or otherwise.
12. Tenuinucellate or crassinucellate.
13. Number of integuments: one or two.

14. Thickness of integuments: two- or multi-layered.
15. Presence or absence of vascular tissue in integuments.
16. Micropyle: formed by inner, outer, or both integuments.
17. Nucellar beak formed or not.
18. Chalaza with hypostase or not.
19. Endothelium formed or not.
20. Archegonium one- or multi-celled.
21. Cytokinesis in a megaspore mother cell: occurs or not.
22. Shape of megaspore tetrads: linear, T-shaped, or otherwise.
23. Position of functional megaspore: micropylar or chalazal.
24. Type of megagametophyte development: *Polygonum*, *Oenothera*, *Penaea*, or other.
25. Fatty globules in megaspores and embryo sacs present or absent.
26. Characteristics of synergids: hooked, pyriform, or otherwise.
27. Characteristics of antipodal cells: persistent or ephemeral. Definitions of the term "persistent" and "ephemeral" were sometimes vague, so in this work the antipodal cells that degenerate and disappear before fertilization are referred to as "ephemeral," whereas those that persist up to fertilization and postfertilization are referred to as "persistent."
28. Number of constituent nuclei or cells in a mature embryo sac: eight (as is usual in the *Polygonum*-type embryo sac), five (due to early disintegration of three antipodal cells in the *Polygonum*-type embryo sac), four (as in the *Oenothera*-type sac), 16 (as in the *Penaea*-type embryo sac), or otherwise.

Seeds:

29. Path of pollen tube: porogamous, chalazogamous, or mesogamous.
30. Type of endosperm formation: nuclear or cellular.
31. Presence or absence of endosperm in mature seed.
32. Type of embryogeny: Onagrad, Solanad, Asterad, or otherwise.
33. Characteristics of suspensor: short, massive, haustorial, or otherwise.
34. Embryo with two equally developed cotyledons or not.
35. Polyembryony common or not.

RESULTS AND DISCUSSION

Our results have been tabulated in order to facilitate comparisons among families (Tables 1–4). Of the families of interest, Crypteroniaceae (*Crypteronia*, *Axinandra*, and *Dactylocladus*), Chrysobalanaceae, and Coridaceae are unknown embryologically. In addition, many unusual and critical genera such as *Alzatea* and *Rhynchocalyx* (Lythraceae), *Strephonema* (Combretaceae), and *Psiloxylon* and *Heteropyxis* (Myrtaceae) are also unknown embryologically. The investigation of these taxa in relation to the characteristics presented in Tables 1–4 obviously is a matter of high priority.

Our embryological analyses, even though they were in most cases based on inadequate information, indicate clearly that many characteristics were consistent within given families (Table 1). Taken as a whole, they have made possible the definition of Myrtales as including a certain group of families linked together by their common possession of a set of shared embryological characteristics. This set of families agrees with that proposed as core Myrtales by Dahlgren and Thorne (1983): Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae. The embryological characteristics common to this set of families are:

(1) Tapetum glandular (Table 2; Penaeaceae and Punicaceae are unknown in this respect).

(2) Ovule crassinucellate (Table 3).

(3) Inner integument two-layered (Table 3). The only known exception among the core families of Myrtales is *Syzygium* (Myrtaceae). Both in its initiation and subsequent early growth, the inner integument is consistently two-layered in all members of Myrtales except *Syzygium*. It forms a marked contrast with the outer integument, the thickness of which not only varies from genus to genus but which also tends to become thicker in the course of development. The analyses of Davis (1966, p. 15) indicated to her that the number of integuments present should be treated either as a generic or as a specific characteristic, but for Myrtales it appears to be of more fundamental significance. It seems clear that the unitegmatic condition of the ovule in *Syzygium* must have originated secondarily within Myrtaceae; the distribution of this feature in the family should be studied further.

(4) Micropyle formed by both integuments

TABLE 1. General information and references of the embryology of Myrtalean and non-Myrtalean families analyzed.

Families	Number of Genera Studied So Far	Level of Knowledge	Selected References
<i>Myrtales</i>			
1. Combretaceae (20/400)	10	50%	Brewbaker (1967); Fagerlind (1941); Karsten (1891); Nagaraj (1954a, 1954b, 1954c, 1955); Pal (1951); Rao (1963); Venkateswarlu (1952b); Venkateswarlu and Rao (1972).
2. Lythraceae (23/500)	13	15%	Brewbaker (1967); Joshi and Venkateswarlu (1935a, 1935b); Smith and Herr (1971); Souèges (1925); Tischler (1917); Venkateswarlu (1937a); Warming (1878); Mauritzon (1934, 1939).
3. Melastomataceae (200/4,000)	19	3%	Brewbaker (1967); Crété (1956, 1957, 1960a, 1960b); Iconomides (1958); Ruys (1925); Subramanyam (1942, 1944, 1946, 1948, 1951); Ziegler (1925).
4. Myrtaceae (140/3,000)	29	9%	Brewbaker (1967); Davis (1968, 1969); Greco (1930); Mauritzon (1939); Narayanaswami and Roy (1960a, 1960b); van der Pijl (1934); Polunina (1957a, 1957b, 1957c, 1958a, 1958b, 1959, 1964); Prakash (1969a, 1969b, 1969c, 1969d, 1973); Roy (1953, 1955, 1960, 1961, 1962a, 1962b); Roy and Sahai (1962); Souèges (1940a); Tiwary and Rao (1934).
5. Oliniaceae (1/8)	1	66%	Mauritzon (1939).
6. Onagraceae (17/675)	12	37%	Beer (1905); Bonnet (1912); Brewbaker (1967); Gates (1911); Geerts (1908, 1909); Haberlandt (1927); Håkansson (1925); Hulbary and Rao (1959); Ishikawa (1918); Johansen (1928a, 1928b, 1929, 1930a, 1930b, 1931a, 1931b, 1931c, 1933, 1934); Kahn (1942); Lebègue (1948a, 1948b); Maheshwari and Gupta (1934); Modilewski (1909); O'Neal (1923); Pagni (1958); Renner (1914, 1921); Seshavaram (1967, 1970); Souèges (1920, 1935, 1946); Subramanyam and Govindu (1948); Täckholm (1914, 1915).
7. Penaeaceae (7/20)	4	38%	Stephens (1909).
8. Punicaceae (1/2)	1	33%	Brewbaker (1967); King (1947); Mauritzon (1939).
9. Sonneratiaceae (2/8)	2	83%	Joshi (1939); Karsten (1891); Mauritzon (1939); Venkateswarlu (1936a, 1936b, 1937b).

TABLE 1. (Continued).

Families	Number of Genera Studied So Far	Level of Knowledge	Selected References
10. Trapaceae (1/15)	1	100%	Brewbaker (1967); Ghosh (1954); Gibelli and Ferrero (1891); Ishikawa (1918); Ram (1956); Trela-Sawicka (1978).
<i>Non-Myrtales</i>			
11. Elaeagnaceae (3/50)	1	33%	Rau and Sharma (1970); Sharma (1966).
12. Elatinaceae (2/40)	2	83%	Dathan and Singh (1971); Frisendahl (1927); Kajale (1939); Lemesle (1929); Raghaven and Srinivasan (1940).
13. Haloragaceae (8/100)	3	38%	Bala-Bawa (1969a, 1969b, 1970); Brewbaker (1967); Kapil (1962); Kapil and Bala-Bawa (1968); Nagaraj and Nijalingappa (1967a, 1967b, 1974); Nijalingappa (1967); Souèges (1940b); Stolt (1928).
14. Lecythidaceae (20/400)	7	13%	Brewbaker (1967); Mauritzon (1939); Treub (1884); Venkateswarlu (1952a).
15. Rhizophoraceae (14/100)	6	12%	Brewbaker (1967); Carey (1934); Cook (1907); Juncosa (1982); Karsten (1891); Mauritzon (1939).
16. Thymelaeaceae (50/500)	18	17%	Brewbaker (1967); Fagerlind (1940); Fuchs (1938); Guérin (1913, 1915); Kausik (1940); Mauritzon (1939); Osawa (1913); Souèges (1942); Strasburger (1884); Venkateswarlu (1945, 1946, 1947a, 1947b); Vesque (1879a, 1879b); Winkler (1904).

(Table 3; except for the unitegmic *Syzygium*). According to Davis (1966, p. 16), in 88 of 189 families of angiosperms the micropyle is formed by the inner integument alone; in 74 families both integuments are involved; and in only four families is the micropyle formed by the outer integument. In the other families, the integumental components of the micropyle are constant within individual genera but vary from genus to genus within the family. These results suggest that variation in the participation of the inner and outer integuments in the formation of the micropyle is an important embryological characteristic with systematic significance. Within Myrtales, the cases of *Guiera senegalensis* (Combretaceae; Venkateswarlu & Rao, 1972), *Darwinia fascicularis* and *D. micropetala* (Myr-

taceae; Prakash, 1969c), *Stenosiphon linifolius* (Onagraceae; Johansen, 1930b), in which the micropyle is apparently formed by the inner integument alone, should be regarded as isolated exceptions. In some of these instances, the formation of the micropyle is probably a secondary characteristic caused by the spatial condition of the ovarian locule (see footnotes 15 and 18 in Table 1). In *Trapa* (Trapaceae) the micropyle is not formed by integuments owing to the production of an elongated nucellar beak. The nucellar beak is evidently a secondary characteristic in angiosperms, and therefore its presence does not hinder the inclusion of Trapaceae in Myrtales.

(5) Antipodal cells absent or, if present, ephemeral (Table 3). Of the families of Myrtales

TABLE 2. Embryological data of anthers.

Families	Number of Sporangia	Anther Wall Development	Anther Epidermis	Endothecium	Middle Layers	Tapetum	Tapetal Cell	Cytokinesis in Meiosis	Microspore Tetrad	Mature Pollen Grain
<i>Myrtales</i>										
1. Combretaceae (20/400)	4	Basic type ex- cept in <i>Guiera sene- galensis</i>	persistent (?)	fibrous	ephemeral	glandular	2-nucleate	simultaneous	tetrahedral or isobilateral	2-celled ¹
2. Lythraceae (23/500)	4	Dicotyledonous type ²	—	fibrous ²	ephemeral ²	glandular ²	2–6-nucleate ²	simultaneous ²	tetrahedral or isobilateral ²	2-celled
3. Melastomataceae (200/4,000)	4	—	persistent	fibrous except in <i>Melasto- ma</i> and <i>Oxyspora</i>	ephemeral ex- cept in <i>Melastoma malabath- ricum</i> ³	glandular	1-nucleate	simultaneous	tetrahedral	3-celled
4. Myrtaceae (140/3,000)	4	Basic type	persistent or ephemeral	fibrous	ephemeral	glandular	2-nucleate, but 1-nu- cleate in <i>Eucalyptus melliodora</i>	simultaneous	tetrahedral or decussate	2-celled
5. Oliniaceae (1/8)	4	—	—	fibrous (?)	ephemeral	glandular	2-nucleate (?)	—	—	—
6. Onagraceae (17/675)	4 or many ⁴	—	persistent	fibrous	ephemeral	glandular	2-nucleate, but multi- nucleate in some species of <i>Oenothera</i> and <i>Fuch- sia</i>	simultaneous	tetrahedral, isobilateral or decussate	2-celled
7. Penaeaceae (7/20)	—	—	—	—	—	—	—	—	—	—
8. Punicaceae (1/2)	—	—	—	—	—	—	—	—	—	2-celled
9. Sonneratiaceae (2/8)	4	Dicotyledonous type	persistent	fibrous	ephemeral	glandular	2-nucleate	—	—	2-celled

TABLE 2. (Continued).

Families	Number of Sporangia	Anther Wall Development	Anther Epidermis	Endothecium	Middle Layers	Tapetum	Tapetal Cell	Cytokinesis in Meiosis	Microspore Tetrad	Mature Pollen Grain
10. Trapaceae (1/15)	4	—	persistent	fibrous	ephemeral	glandular	multi-nucleate	simultaneous	tetrahedral or decussate	2-celled
<i>Non-Myrtales</i>										
11. Elaeagnaceae (3/50)	4	—	—	fibrous	ephemeral	glandular	2-4-nucleate	—	tetrahedral or decussate	3-celled
12. Elatinaceae (2/40)	4	Basic type	persistent	fibrous	ephemeral	glandular	2-nucleate in <i>Bergia</i> but 2-4-nucleate in <i>Elatine</i>	simultaneous	tetrahedral or isobilateral	2-celled in <i>Bergia</i> , but 3-celled in <i>Elatine</i>
13. Haloragaceae (8/100)	4	Monocotyledonous type	persistent	fibrous	ephemeral	glandular	1-5-nucleate	simultaneous	tetrahedral or decussate	3-celled
14. Lecythidaceae (20/400)	—	—	—	fibrous	ephemeral	amoeboid	2-nucleate	—	—	2-celled or 3-celled
15. Rhizophoraceae (14/100)	—	—	—	—	—	—	—	—	—	2-celled
16. Thymelaeaceae (50/500)	4	Monocotyledonous or Basic type	persistent	fibrous	ephemeral	glandular	2-nucleate, but 2-6-nucleate in <i>Wikstroemia</i>	simultaneous	tetrahedral or isobilateral	3-celled

¹ Pal (1951) reported the three-celled condition in *Terminalia catappa*, the only report which described this condition in Combretaceae. Other papers on *Terminalia catappa* (Nagaraj, 1954c; Venkateswarlu & Rao, 1972) and on other species of *Terminalia* (Nagaraj, 1954a; Venkateswarlu & Rao, 1972; Brewbaker, 1967) reported only the two-celled conditions.

² Based only on *Ammannia baccifera* (Joshi & Venkateswarlu, 1936).

³ According to Subramanyam (1948), five to seven middle layers are formed in *Melastoma melabathricum*, the upper two or three persisting and the remainder ultimately crushed.

⁴ *Calylophus*, *Clarkia*, *Gaura*, *Hauya*, *Heterogaura*, and two species of *Ludwigia* have polysporangiate anthers in which microsporogenous tissue is divided by sterile septa into many distinct packets (Raven, 1969; Eyde, 1978).

TABLE 3, part A. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part B, beginning on page 80, for additional characters; see page 82 for footnotes.

Families	Curvature ¹	Nature of Nucellus	Number of Integuments	Thickness of Integuments ²	Vasculature of Integuments	Micropyle Formation	Nucellar Beak	Hypostase
<i>Myrtales</i>								
1. Combretaceae (20/400)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered in most genera but 3-layered in <i>Terminalia</i> and <i>Bucida</i>	absent	i.i. and o.i. but only i.i. in <i>Guiera senegalensis</i>	not formed	present in some genera
2. Lythraceae (23/500)	anatropous	crassinucellate ⁸	2	i.i. 2-layered; o.i. 2-layered in most genera but 5-layered in <i>Cuphea</i>	absent	i.i. and o.i.	not formed	absent except in <i>Ammannia</i>
3. Melastomataceae (200/4,000)	anatropous, or campylotropous (<i>Memecylon</i>)	crassinucellate	2	i.i. 2-layered; o.i. 2-3-layered	absent	i.i. and o.i.	not formed	absent
4. Myrtaceae (140/3,000)	anatropous	crassinucellate	2, but only 1 in <i>Syzygium</i> ⁹	i.i. 2-layered; o.i. 2-layered in most genera but 2-4-layered in several genera	present in the single integument in <i>Syzygium</i>	i.i. and o.i. with a few exceptions ¹⁰	not formed	present in some genera
5. Oliniaceae (1/8)	campylotropous	crassinucellate	2	i.i. 2-layered; o.i. 4-layered	present in o.i.	i.i. and o.i.	not formed	absent
6. Onagraceae (17/675)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2- or multi-layered	absent	i.i. and o.i., but i.i. in <i>Stenosiphon</i> ¹²	not formed	present in most genera
7. Penaeaceae (7/20)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	—
8. Punicaceae (1/2)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 4-layered	absent	i.i. and o.i.	not formed	absent

TABLE 3, part A, continued from page 78. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part B, beginning on page 80, for additional characters; see page 82 for footnotes.

Families	Curvature ¹	Nature of Nucellus	Number of Integuments	Thickness of Integuments ²	Vasculature of Integuments	Micropyle Formation	Nucellar Beak	Hypostase
9. Sonneratiaceae (2/8)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	absent
10. Trapaceae (1/15)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 5-14-layered	absent	not formed	formed	present
<i>Non-Myrtales</i>								
11. Elaeagnaceae (3/50)	anatropous	crassinucellate	2	—	—	—	not formed	present
12. Elatinaceae (2/40)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	absent
13. Haloragaceae (8/100)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	present
14. Lecythidaceae (20/400)	anatropous	tenuinucellate	2	i.i. multi-layered; o.i. multi-layered	present in o.i.	i.i.	not formed	absent
15. Rhizophoraceae (14/100)	anatropous	crassinucellate	2	i.i. massive; o.i. massive	present in o.i. in some genera	i.i. and o.i. in <i>Bruguiera</i> and <i>Rhizophora</i> ; only i.i. in <i>Gynotroches</i> ; not formed in <i>Anisophyllea</i> (?)	formed in <i>Anisophyllea</i>	—
16. Thymelaeaceae (50/500)	anatropous	crassinucellate	2	i.i. 3-4-layered; o.i. 3-4-layered	absent	i.i.	not formed	present in many species

TABLE 3, part B. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part A, beginning on page 78, for additional characters; see page 82 for footnotes.

Families	Endothelium	Archeporium ³	Cytokinesis in Meiosis	Megaspore Tetrad ⁴	Functional Megaspore ⁵	Pattern of Embryo Sac Formation	Fatty Globules in Megaspores and Embryo Sacs	Synergids	Antipodal Cells	Number of Nuclei in Mature Embryo Sac
<i>Myrtales</i>										
1. Combretaceae (20/400)	not formed	1-celled ⁶	occurs	linear	chalazal cell	<i>Polygonum</i> type ⁷	absent	hooked and pyriform	ephemeral, but persistent in <i>Guiera sene- galensis</i>	5, but 8 or more in <i>Guiera se- negalensis</i>
2. Lythraceae (23/500)	not formed	multi-celled; only one functions	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	hooked	ephemeral	5
3. Melastomataceae (200/4,000)	not formed	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	hooked	ephemeral	5
4. Myrtaceae (140/3,000)	not formed ¹¹	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent, but present in <i>Psidium</i> <i>guajava</i>	diverse in form	ephemeral	5
5. Oliniaceae (1/8)	not formed	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	—	ephemeral	5
6. Onagraceae (17/675)	not formed	1-celled	occurs	linear	micropylar cell	<i>Oenothera</i> type	absent	filiform	absent	4
7. Penaeaceae (7/20)	not formed	1-celled	does not occur	decussate ¹³	all 4 nuclei	<i>Penaea</i> type	absent	—	absent	16
8. Punicaceae (1/2)	not formed	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	elongated	ephemeral	5
9. Sonneratiaceae (2/8)	not formed	multi-celled; only one functions	occurs	linear	chalazal cell	<i>Polygonum</i> type	present in <i>Sonneratia</i> but absent in <i>Duaban- ga</i>	hooked	ephemeral	5

TABLE 3, part B, continued from page 80. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part A, beginning on page 79, for additional characters; see page 82 for footnotes.

Families	Endothelium	Archegonium ³	Cytokinesis in Meiosis	Megaspore Tetrad ⁴	Functional Megaspore ⁵	Pattern of Embryo Sac Formation	Fatty Globules in Megaspores and Embryo Sacs	Synergids	Antipodal Cells	Number of Nuclei in Mature Embryo Sac
10. Trapaceae (1/15)	not formed	1-2-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	pyriform	ephemeral	5
<i>Non-Myrtales</i>										
11. Elaeagnaceae (3/50)	—	1-3-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	—	ephemeral	5
12. Elatinaceae (2/40)	not formed	multi-celled; only one functions	occurs	linear or T-shaped	chalazal cell	<i>Polygonum</i> type	absent	hooked and pyriform in <i>Bergia am- manioides</i>	ephemeral	8
13. Haloragaceae (8/100)	not formed	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	hooked and pyriform	persistent	8
14. Lecythidaceae (20/400)	formed in many species ¹⁴	multi-celled; only one functions	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	pyriform	ephemeral	5
15. Rhizophoraceae (14/100)	formed in <i>Carallia</i> , <i>Gyno- troches</i> , <i>Bruguiera</i> and <i>Cas- sipourea</i>	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	pyriform	ephemeral in <i>Ceriops</i> but persistent in <i>Gynotroches</i>	5 or 8
16. Thymelaeaceae (50/500)	not formed	1-celled	occurs	linear	chalazal cell	<i>Polygonum</i> type	absent	hooked, rarely filiform (<i>Daphne can- nabina</i>)	persistent; cells usually ampli- fy (up to as many as 30 in <i>Thymelaea arvensis</i>)	8 or more

TABLE 3, parts A & B, concluded. Footnotes.

¹ Predominant or usual condition.

² Based on the original thickness of integuments seen at the initiation and early growing stage.

³ Predominant or usual condition.

⁴ Predominant or usual condition.

⁵ Predominant or usual condition.

⁶ Venkateswarlu (1952) described that a multi-celled archesporium was common in *Poivrea coccinea* (= *Combretum coccinea*), and Nagaraj (1954c, 1955) also reported the common occurrence of a multi-celled archesporium in *Terminalia catappa* and *T. belerica*. Therefore, Davis (1966, p. 87) described that "commonly several archesporial cells differentiate" in Combretaceae. In contrast, other more recent papers by Rao (1963) and by Venkateswarlu and Rao (1972), the latter of which dealt with 18 species in 9 genera (including *Terminalia* and *Combretum*), made it clear that the one-celled archesporium is common and the multi-celled one (i.e., consisting of two or more cells) is rare.

⁷ Mauritzon (1939) reported the 16-nucleate *Penaea*-type embryo sac in two species of *Combretum*, *C. paniculatum* and *C. pincianum*. These results need to be reconfirmed because other authors have reported only *Polygonum*-type embryo sacs in *Combretum*. Variation in female gametophyte formation is known in some genera, however (see Hjelmquist, 1964), for review.

⁸ Smith and Herr (1971, p. 198), contrary to many other authors, stated that "the nucellus of *Ammannia coccinea* was tenuinucellate." But tenuinucellate ovules have never been reported in other species of *Ammannia* nor in other Lythraceae. The drawings of sections of ovules (Smith & Herr, 1971, p. 167, Figs. 4 and 5) which they intended to document the existence of tenuinucellate condition of this species indicate rather that their material was clearly crassinucellate; the subhypodermal cells that they identified with the archesporial cells are evidently megaspore mother cells cut off from the actual archesporial cells.

⁹ Besides the species of *Syzygium*, *Eugenia paniculata* (Mauritzon, 1939), *E. jambos* (Pijl, 1934), *E. malaccensis* (Pijl, 1934; Roy, 1960), *E. fruticosa* (Roy, 1961) and *E. myrtifolia* (Roy, 1962b) are reported to have a unitegmatic ovule. But all of these *Eugenia* are assigned to *Syzygium* (sensu Schmid, 1972): according to Schmid (pers. comm.), *Eugenia paniculata* is assigned to *Syzygium paniculatum* Gaertner, *Eugenia jambos* to *Syzygium jambos* (L.) Alston, *Eugenia malaccensis* to *Syzygium malaccense* (L.) Merr. & Perry, *Eugenia fruticosa* to *Syzygium fruticosum* DC., and *Eugenia myrtifolia* to *Syzygium myrtifolium* (Roxb.) DC. On the other hand, *Eugenia bracteata*, which should remain in *Eugenia* sens. str. sensu Schmid, has a bitegmatic ovule (Roy, 1955).

¹⁰ Mauritzon (1939, p. 110) states that "it appears that it is not unusual in the Myrtaceae for the micropyle to be formed entirely or mainly by the inner integument." In fact, *Darwinia fascicularis* and *D. micropetala* have the micropyle formed by the inner integument alone (Prakash, 1969c), whereas *Darwinia taxifolia* has one formed by both integuments (Mauritzon, 1939). Thus there is variation even within the genus *Darwinia* in the participation of integuments in the formation of the micropyle. The secondary growth of the inner integument combined with the suppression of growth of the outer integument because of the limited space available within the ovarian locule may result in the formation of the micropyle by the inner integument only. In both species of *Darwinia* that have the micropyle formed by the inner integument only, the inner integument develops into "collar-like lips" (Prakash, 1969c), a condition that clearly seems to be secondary.

¹¹ Endothelium has not been reported in references, but in *Leptospermum*, *Kuntzea*, *Agonis*, *Callistemon*, and *Melaleuca*, the upper part of the nucellus tends to be destroyed by the growth of the embryo sac, a feature that would normally accompany the development of an endothelium. In *Melaleuca* particularly, the mature embryo sac borders directly on the inner integument (Mauritzon, 1939).

¹² In *Stenosiphon linifolius* the micropyle is formed by the extremely elongated "beak-like process" of the inner integument (Johansen, 1930b) a characteristic that seems to be secondary in the family.

¹³ Cell walls are absent, but four megaspore nuclei are arranged in such a way that one lies at the top, one lies at the bottom, and the other two lie at the sides. The decussate arrangement is acquired by oblique divisions of the micropylar nucleus and of the chalazal nucleus that were formed by meiosis I, and not by a combination of vertical and transverse divisions.

¹⁴ According to Mauritzon (1939), an endothelium (called a "mantle layer" by him) is formed in *Couroupita guianensis*, *Careya arborea*, and *Barringtonia speciosa* but not in other species of *Barringtonia* nor in *Gustavia angusta*. Venkateswarlu (1952) reported its occurrence both in *Napoleona imperialis* and in *Barringtonia acutangula*. The absence of an endothelium in some species of *Barringtonia* and *Gustavia* should be reconfirmed, because the presence of endothelium is otherwise a family characteristic of Lecythidaceae (Davis, 1966, p. 16). Probably Mauritzon's observations had not extended to old enough stages of ovule development to observe the endothelium and it is likely that it is present in all members of Lecythidaceae.

mentioned above, all except Onagraceae and Penaeaceae consistently have ephemeral antipodal cells that degenerate and disappear before fertilization. In these families, therefore, the mature embryo sac comprises only five nuclei or cells: an egg; two synergids; and two polar nuclei, which may fuse into a secondary nucleus before fertilization. This relationship suggests that for Myrtales the antipodal cells are unnecessary in the organized mature embryo sac. Exceptionally, the antipodal cells of *Guiera senegalensis* (Combretaceae) persist into the postfertilization phase, a feature that is regarded as unique for Combretaceae (Venkateswarlu & Rao, 1972). In Onagraceae and Penaeaceae, antipodal cells are absent throughout megagametophyte development. In the 16-nucleate *Penaea*-type embryo sac, one might regard the three chalazal cells as corresponding to the antipodal cells. Stephens (1909) mentioned, however, that these three chalazal cells resembled an egg apparatus more or less closely. In fact, the three chalazal cells are produced in the same way as the three cells of a true micropylar egg apparatus, but from a different megaspore nucleus.

(6) Nuclear-type endosperm formation (Table 4).

(7) Exalbuminous seed (Table 4).

Core Myrtales

Taken together, these features characterize the core Myrtales group defined by Dahlgren and Thorne (1983). Within this assemblage, Lythraceae are further characterized (except for *Punica*) by having a multi-celled archesporium in the ovule, a feature that is not common elsewhere in the order. Although this characteristic has in general received less attention than other embryological features, it does appear to have some value at least in particular cases. Thus, Vijayaraghavan (1970) adopted it as one of the bases for the exclusion of *Paeonia* from Ranunculaceae.

Sonneratia and *Duabanga*, usually taken as constituting a separate family Sonneratiaceae, agree with other Lythraceae in having a multi-celled archesporium. Embryologists as well as other students of plant systematics have in general argued for a close relationship among these groups (Joshi, 1939; Venkateswarlu, 1936a, 1936b, 1937b). In agreement with these observations, our analysis of the embryological literature offers no basis for distinguishing between them, and supports their inclusion in a single

family (Dahlgren & Thorne, 1983). *Sonneratia* and *Duabanga* differ in that the former consistently has fatty globules in its megaspores and embryo sacs whereas these are lacking in *Duabanga* (Karsten, 1891; Venkateswarlu, 1937b; Mauritzon, 1939). This accords with certain other lines of evidence in suggesting that these genera may not be directly related to one another.

Punica differs from other Lythraceae in having a uni-celled archesporium, and a thick multi-layered outer integument. Nonetheless, it is included in Lythraceae by Dahlgren and Thorne (1983). Further embryological studies on *Punica* are clearly needed.

Although many of the embryological characteristics of Penaeaceae are unknown, those that have been investigated clearly warrant inclusion of this unusual South African family in Myrtales. The only distinctive feature among those that have been reported is the characteristic 16-nucleate *Penaea*-type embryo sac. This type of embryo sac development is characterized by the fact that meiosis in the megaspore mother cell is not accompanied by cytokinesis. Following meiosis, all four of the decussately arranged megaspore nuclei function, each dividing twice to produce four nuclei or cells. The quartet associated with the true micropylar egg apparatus is always derived from the micropylar megaspore nucleus (Stephens, 1909). In both the frequency of division of the megaspore nucleus and the origin of the egg apparatus, the *Penaea*-type embryo sac development resembles the *Oenothera*-type of embryo sac development that is characteristic of Onagraceae, discussed below (see also Maheshwari, 1948).

Melastomataceae exhibit a distinctive embryological feature that is unknown elsewhere in the order, uni-nucleate anther tapetum cells in place of the bi- or multi-nucleate ones characteristic of other families of Myrtales. In addition, Melastomataceae are the only family of Myrtales in which the endothecium sometimes develops fibrous thickenings. Another distinctive feature that has been claimed for Melastomataceae is three-celled mature pollen, in place of the two-celled mature pollen characteristic of all other families of Myrtales. A careful review of the few published reports, however, has indicated that Melastomataceae, like all other core Myrtales, have two-celled mature pollen (Tobe & Raven, in prep.). In this connection, it seems to be worthwhile to note the fact that the pollen cell con-

TABLE 4. Embryological data of seeds.

Families	Path of Pollen Tube	Endosperm Formation	Endosperm in Mature Seed	Embryogeny	Suspensor	Embryo	Polyembryony
<i>Myrtales</i>							
1. Combretaceae (20/400)	porogamous	Nuclear type	absent	Asterad type	short and small	2 cotyledons with same size	rare
2. Lythraceae (23/500)	porogamous	Nuclear type	absent ¹	Onagrad type ¹	short and small ¹	2 cotyledons with same size	absent
3. Melastomataceae (200/4,000)	porogamous	Nuclear type	absent	Onagrad type	short and massive	2 cotyledons with same size	occasional
4. Myrtaceae (140/3,000)	porogamous	Nuclear type	absent	Onagrad type	short and small, or absent	2 cotyledons with same size	usual in <i>Syzygium</i>
5. Oliniaceae (1/8)	—	Nuclear type	—	—	—	—	—
6. Onagraceae (17/675)	porogamous	Nuclear type	absent	Onagrad type	short and small	2 cotyledons with same size	rare
7. Penaeaceae (7/20)	porogamous	Nuclear type	absent	Asterad type	absent	2 cotyledons with same size	—
8. Punicaceae (2/8)	—	Nuclear type	—	—	—	—	—
9. Sonneratiaceae (2/8)	porogamous	Nuclear type	absent	Onagrad type	short and small	2 cotyledons with same size	absent
10. Trapaceae (1/15)	porogamous	Nuclear type	absent	Solanad type	long, coiled, haustorial; the upper part forming collar	2 cotyledons with extremely different size	absent

TABLE 4. (Continued).

Families	Path of Pollen Tube	Endosperm Formation	Endosperm in Mature Seed	Embryogeny	Suspensor	Embryo	Polyembryony
<i>Non-Myrtales</i>							
11. Elaeagnaceae (3/50)	—	Nuclear type	absent	Asterad type	short and massive	2 cotyledons with same size	absent
12. Elatinaceae (2/40)	—	Nuclear type	present	Solanad type	short and small	2 cotyledons with same size	absent
13. Haloragaceae (8/100)	porogamous	Nuclear type in <i>Laurembergia</i> but Cellular type in <i>Haloragis</i> and <i>Myriophyllum</i> ²	present	Caryophyllad type	2-celled, enlarged, haustorial	2 cotyledons with same size	absent
14. Lecythidaceae (20/400)	—	Nuclear type	—	—	short and massive in <i>Barringtonia vriesii</i>	—	—
15. Rhizophoraceae (14/100)	porogamous	Nuclear type	present	—	short and massive, or long	2 cotyledons with same size	rare
16. Thymelaeaceae (50/500)	porogamous	Nuclear type	present ³	Asterad type	short and small, or absent	2 cotyledons with same size	rare

¹ Based only on *Duabanga sonneratioides* (Venkateswarlu, 1937b).² Even in the Nuclear type, cell wall formation commences as early as the 8-nucleate stage (Bala-Bawa, 1969a; Nagaraj & Nijalingappa, 1974), a phenomenon that demonstrates a strong tendency towards the Cellular type.³ According to Guérin (1915), in Thymelaeaceae seeds that completely lack endosperm are rather exceptional. Even in the species of *Phaleria* which nearly lack endosperm, two- to five-layered endosperm tissue was present on the surface of the cotyledons in the mature seed.

dition is highly consistent in the order (cf. Brewbaker, 1967). The pollen cell condition of Melastomataceae should be studied further.

Although little is known about the embryology of Oliniaceae, what is known clearly supports their inclusion within Myrtales, as do their other features (Rao & Dahlgren, 1969). The only known distinctive feature is the thick, vascularized outer integument. Closer comparisons with Melastomataceae ought to be made when more information is available, following the suggestions of Rao and Dahlgren (1969); the comparisons with Thymelaeaceae and Rubiaceae suggested by these authors cannot be taken as indications of genuine relationship in view of the embryological and other features of *Olinia*.

Combretaceae have been studied as extensively from an embryological point of view as any family of Myrtales. *Guiera* differs in several respects from the other members of the family and indeed stands out within Myrtales, but in general, Combretaceae agree closely in their embryological features with other Myrtales. *Guiera* differs from all other Myrtales in having persistent antipodal cells and a micropyle formed by the inner integument only (Venkateswarlu & Rao, 1972). Based on these features, Venkateswarlu and Rao (1972), taking into account also evidence from floral morphology and anatomy, proposed the establishment of a unigeneric tribe, Guierae, for *Guiera*. In its overall features, however, *Guiera* clearly fits into the subtribe Combretinae together with *Combretum* and other genera (Stace, 1965; Exell & Stace, 1966, 1972), so that its unusual embryological attributes must almost certainly be secondary. The persistence of antipodal cells, which multiply after fertilization, seems clearly to be secondary, and it appears logical to consider the lack of participation of the outer integument in the formation of the micropyle secondary also.

From an embryological point of view, Trapaceae are the most distinctive family included in Myrtales. A long nucellar beak is formed in *Trapa* as a result of an extension of the apex of the nucellus. The formation of this beak evidently precludes direct participation of the integuments in the formation of the micropyle. A second very distinctive feature of *Trapa* is the long, coiled haustorial suspensor, the upper part of which forms a collar supporting the embryo proper. A third distinctive feature is the asymmetrical embryo, which has two very unequal cotyledons. Some or all of these features might

be related to the aquatic habitat of the family but this suggestion needs further evaluation. Other embryological characteristics of this monogeneric family include the thick, nonvascularized outer integument and the multinucleate anther tapetal cells. The embryological characteristics of Trapaceae do not support a direct relationship either with Onagraceae (a family in which Trapaceae were formerly included) or with Lythraceae (contrary to the views of Miki, 1959).

Myrtaceae, like Combretaceae, have few distinctive features that discriminate them from other Myrtales. *Syzygium* is unique in the order in its unitegmic ovules. Doubtless this represents a derived feature as it does in angiosperms generally (Bouman, 1977), and it probably will be found in other genera when the family is better known embryologically. Mauritzon (1939, p. 102–103) stated that in "*Eugenia paniculata*" (= *Syzygium paniculatum*) "two two-layered integuments have fused together to form a single integument of four layers." Unitegmy could also be derived by the loss of one of the two integuments. A third way in which unitegmy could be derived has recently been suggested by Bouman (1977) and Bouman and Schier (1979). These authors have concluded that both in Ranunculaceae and in Gentianaceae unitegmy has originated following a complicated process involving the fusion of the primordia that has led to a shifting of the inner integument and an arrested development of it subsequently. If unitegmy has originated in this way in *Syzygium*, a major part of its single integument would be composed of the outer integument. This integument might then represent an ancestral form of outer integument in Myrtaceae, as suggested by its thickness and possession of a vascular supply. Regardless of the exact method of derivation however it appears virtually certain that unitegmy in *Syzygium* has been derived from bitegmy within Myrtaceae because the genus is not otherwise remarkable within the family. The distribution of unitegmy in Myrtaceae should be investigated further.

Onagraceae are characterized by their distinctive 4-nucleate *Oenothera*-type embryo sac, unknown elsewhere in angiosperms. This family has been considered to have a close relationship to Lythraceae, and several embryologists such as Tischler (1917), Mauritzon (1934), and Joshi and Venkateswarlu (1936) considered that the Lythraceous embryo sac with ephemeral antipodal cells forms phylogenetically an intermediate stage

between the 4-nucleate embryo sac of Onagraceae and the normal 8-nucleate embryo sac. In fact, ephemeral antipodal cells are common to most members of the order Myrtales, and the condition in Lythraceae cannot, therefore, be taken as indicative of a direct relationship between this family and Onagraceae. The Onagrad-type embryogeny common to both families occurs in Myrtaceae and Melastomataceae as well. Thus none of the embryological attributes of Onagraceae suggests a particular relationship either to Lythraceae or to any other family. Embryologically, the relationship between the 4-nucleate *Oenothera*-type of embryo sac in Onagraceae and the 16-nucleate *Penaea*-type embryo sac in Penaeaceae appears to be of more interest, and perhaps more suggestive of a direct relationship. These types of embryo sac development resemble one another in that antipodal cells are not formed at all during megagametogenesis and also in that the micropylar megaspore nucleus in both families divides only twice to form an egg apparatus (see also Maheshwari, 1948). Although these similarities may have originated as a result of convergent evolution, they do at least indicate that the loss of the antipodal cells by omission of the third nuclear division in megagametogenesis has occurred twice in Myrtales, since Penaeaceae and Onagraceae are manifestly not related directly to one another. At present, we suggest that ephemeral antipodal cells constitute a primitive condition in Myrtales that was present in the common ancestor.

Evaluation of Other Families

Among the families that have been thought to be related to or possibly included within Myrtales, we shall discuss first Haloragaceae. Haloragaceae share with the core Myrtales the following features: glandular tapetum; crassinucellate ovule; 2-layered inner integument; and micropyle formed by both integuments. Haloragaceae differ fundamentally from Myrtales, however, in having (1) persistent antipodal cells; (2) either Cellular- or Nuclear-type endosperm formation (Nuclear-type endosperm formation in Haloragaceae when present closely resembles the Cellular-type endosperm formation); (3) albuminous seeds. In addition, Haloragaceae differ from core Myrtales in exhibiting the Monocotyledonous-type of anther wall formation; Caryophyllad-type embryogeny; and a 2-celled, enlarged haustorial suspensor. This type of haustorial suspensor may be related to the ad-

aptation of Haloragaceae to a more or less aquatic habitat. In this connection it may be noted that Trapaceae, which are also strictly aquatic, also have a very distinctive type of haustorial suspensor. Taken together, these embryological features virtually exclude the possibility of any direct relationship of Haloragaceae with Myrtales.

Insufficient information concerning Rhizophoraceae (including Anisophylleaceae) is available to characterize the family or its constituent parts. Notwithstanding this, in their massive inner integument and albuminous seeds, Rhizophoraceae differ sharply from Myrtales. The available embryological information indicates a considerable heterogeneity within the family and might be taken to support the contention that it should be divided into two or more families, which might not be related directly to one another. In *Bruguiera* and *Rhizophora* (Rhizophoreae) the micropyle is formed by both integuments (Cook, 1907; Carey, 1934; Mauritzon, 1939), and in *Gynotroches* (Gynotrocheae) it is formed by the inner integument alone (Mauritzon, 1939). In *Anisophyllea* (Anisophylleae) the extension of the nucellar apical tissue (? = nucellar beak) prevents the formation of the micropyle by integuments (Karsten, 1891). Furthermore, an endothelium is formed in *Carallia* and *Gynotroches* (Gynotrocheae; Karsten, 1891; Mauritzon, 1939), *Cassipourea* (Macarisieae; Juncosa, 1982) and in *Bruguiera* (Rhizophoreae; Mauritzon, 1939) but not in the other genera. The antipodal cells are ephemeral in *Ceriops* and *Bruguiera* (Rhizophoreae) but persistent in *Gynotroches* (Gynotrocheae; Karsten, 1891; Mauritzon, 1939). The outer integument is vascularized in *Rhizophora*, *Ceriops*, and *Bruguiera* (Rhizophoreae; Carey, 1934; Mauritzon, 1939), but probably not in the other tribes. The endothelium and the nature of the integuments that form the micropyle appear to be characteristic of Rhizophoraceae at the family level (Davis, 1966). Those members of Rhizophoraceae with persistent antipodal cells differ from Myrtales in this respect. Further detailed study on the embryology of the various genera of Rhizophoraceae should be valuable in evaluating the apparent heterogeneity of this family.

Thymelaeaceae differ from Myrtales in possessing (1) a thick, 3- to 4-layered inner integument; (2) micropyle formed by the inner integument alone; (3) persistent antipodal cells that often multiply; and (4) albuminous seeds. Em-

bryologically, these differences are decisive in ruling out any direct relationship between Thymelaeaceae and core Myrtales.

Lecythidaceae have many distinctive features embryologically. They are: (1) an amoeboid anther tapetum; (2) tenuinucellate ovule; (3) a thick, multi-layered inner integument; and (4) micropyle formed by the inner integument alone. In addition, the family is characterized by having an endothelium (Mauritzon, 1939). This combination of features seems decisive in precluding any direct relationship between Lecythidaceae and Myrtales.

Although its two constituent genera differ in several respects, Elatinaceae agree with Myrtales in many embryological features. Among them are the glandular anther tapetum; crassinucellate ovule; a 2-layered inner integument; a micropyle formed by both integuments; ephemeral antipodal cells; and Nuclear-type endosperm formation. The only known embryological difference between Elatinaceae and Myrtales concerns the albuminous seeds of Elatinaceae compared with the exalbuminous seeds of Myrtales. Friessdahl (1927) observed a one-layered endosperm in ripe seeds of *Elatine* spp. Dathan and Singh (1971) observed a three- to five-layered endosperm in mature seeds of both *Bergia odorata* and *B. ammannioides* and a one- to two-layered one in those of *B. aestivosa*; in contrast, Raghaven and Srinivasan (1940) did not observe endosperm in the mature seeds of *Bergia capensis*.

Despite the difference in persistence of endosperm, on the basis of embryological features alone we would suggest that Elatinaceae might be placed adjacent to core Myrtales. The classifications of Takhtajan (1980) and Cronquist (1981) regard Elatinaceae as having a close relationship with Clusiaceae-Hypericoideae. Embryologically, Hypericoideae differ markedly from Elatinaceae in having tenuinucellate ovules and an endothelium, and we suggest that this relationship suggested by Takhtajan and Cronquist is probably incorrect.

Elaeagnaceae have been studied very inadequately from an embryological point of view. Not enough information is available, particularly concerning the integuments, to evaluate properly the possibility of a relationship between the Elaeagnaceae and Myrtales on that basis. Available information indicates that Elaeagnaceae share the following embryological features with Myrtales, however: glandular anther tapetum;

crassinucellate ovule; ephemeral antipodal cells; Nuclear-type endosperm formation; and exalbuminous seeds. The embryology of Elaeagnaceae should be studied in more detail and the possibility of a relationship of this family with Myrtales should be evaluated further in the light of this information.

In summary, Myrtales are clearly circumscribed by embryological evidence to include Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae. We further suggest that the possibility of a direct relationship between Elatinaceae and Myrtales is supported by embryological data and should be investigated further from a number of other points of view.

Within Myrtales, the large families Myrtaceae and Combretaceae seem not to be distinctive and to agree with the generalized characteristics of the order in their embryological features. Lythraceae (including Punicaceae and Sonneratiaceae) seem to form another relatively generalized group within the order, standing apart somewhat from Myrtaceae and Combretaceae in their multi-celled archesporium. This multi-celled archesporium might be taken either as a secondary or as a primary characteristic, and its nature should be investigated further in the context of phylogenetic studies of the group. Melastomataceae deviate from all other families of Myrtales in the characteristics of their anthers. Penaeaceae and Onagraceae, although the latter are much more generalized than the former in their embryological characteristics, are both relatively specialized in their loss of antipodal cells. Three small families of Myrtales that otherwise seem not to be directly related to one another—Oliniaceae, Punicaceae (included by Dahlgren & Thorne, 1983, in Lythraceae), and Trapaceae—share with one another a thick, multi-layered outer integument. Students who have recently considered the evolution of integuments, especially Bouman and his colleagues, have generally considered that the evolutionary trend in the integuments of angiosperms proceeds from a thick to a thin integument (see Boesewinkel, 1981). If this relationship is accepted, then it would be assumed that Oliniaceae, Punicaceae, and Trapaceae may retain the primitive integumental condition for Myrtales. In that case, Punicaceae, although they might still legitimately be regarded as belonging in Lythraceae, might be viewed as a distinctive, archaic offshoot within that family.

Trapaceae are more distinctive in their embryology than any other family of Myrtales and differ more from the core Myrtales in their embryological features than do Elatinaceae.

FUTURE DIRECTIONS FOR RESEARCH

More embryological information about Myrtales should prove useful in elucidating further the relationships of the families of the order in the future, and in turn in evaluating the relationships of this order to other groups of angiosperms. Even though the available embryological evidence has allowed a clear circumscription of Myrtales on embryological grounds alone, our comparisons of many taxa are based on incomplete information. It is particularly critical that no information at all has been available on a number of very interesting genera of Myrtales such as: *Alzatea*, *Axinandra*, *Crypteronia*, *Dactylocladus*, and *Rhynchocalyx*, one, several, or all of which may constitute Crypteroniaceae (Van Beusekom-Osinga & Van Beusekom, 1975; van Vliet, 1975; van Vliet & Baas, 1975; Muller, 1975; Cronquist, 1981; Dahlgren & Thorne, 1983). It is likewise unfortunate that no information has been available on *Strephonema*, a very distinctive genus in Combretaceae (Dahlgren & Thorne, 1983). Only a little information is available on *Heteropyxis* and *Psiloxylon*, genera that might be regarded as constituting distinct families or be included within Myrtaceae depending upon one's point of view (Schmid, 1980). Even though all of these genera clearly belong within the order Myrtales, a study of their embryology has the potential of contributing much to our overall understanding of the elements within this order.

In addition, Oliniaceae, Penaeaceae, and Punicaceae are poorly known embryologically, and more information is necessary for a proper evaluation of their status and relationships. Even Melastomataceae and Myrtaceae, for which the level of knowledge from an embryological point of view was estimated as only 3% and 9% respectively, should be studied more extensively. Since these are the two largest families of the order, an examination of their embryological attributes is critical.

Among the groups that have been included within or said to be related to Myrtales, no detailed embryological information is available concerning Chrysobalanaceae and Coridaceae. Chrysobalanaceae are sometimes considered to

be closely allied to the ancestor of Myrtales because of their possession of many common features (Dahlgren & Thorne, 1983). Dahlgren and Thorne (1983) indicated a few gross embryological features of these families including the fact that in Chrysobalanaceae the ripe seeds are exalbuminous, and in Coridaceae, the ovules are bitegmic and tenuinucellate. As regards Rhizophoraceae, embryological evidence suggests a considerable degree of heterogeneity, which accords with the conclusions of Dahlgren and Thorne (1983) and others about the basic heterogeneity of the family. Detailed information about the embryology of the constituent parts of Rhizophoraceae *sens. lat.* would no doubt contribute in an important manner to the resolution of the problem of relationships of Rhizophoraceae and the proper constituency of this family.

A few comments on the references we consulted during the course of preparation of this paper are now appropriate. Most of these references were incomplete, even though the respective authors might have drawn a great deal more from the materials that they had available at the time they conducted their studies. Traditionally, embryological studies have been directed much more closely to the development of the gametophyte than to other features of great systematic interest such as the development of the nucellus and that of the integuments. As mentioned above, very few studies refer to the thickness of the integuments except in descriptions of the structure of seed coats. Despite this, a proper understanding of the thickness of the integuments seems clearly to be of some value as an indicator of affinity and phylogenetic advancement of respective groups. The thickness of secondarily amplified integuments seems to be of less interest as a systematic characteristic than is the original thickness as the integuments are initiated and starting to grow. The thickness of mature integuments is directly related to the structure of the mature seed coats, which may be highly diverse even within a single genus or a group of related genera; e.g., "*Eucalyptus*" (Gaubert & Pryor, 1958, 1959, 1961). More information about the thickness of the integuments and their structure before they begin to thicken during the course of seed coat formation will probably prove to have considerable significance for systematic comparisons. In this connection, Bouman (1971, p. 175) stated that "seemingly identical multi-layered integuments (such as those of Juglandaceae and Liliiflorae) originate by means of different on-

togenetic processes" and that "characters derived from the structure of mature seed coats are of doubtful taxonomic significance at and above the family level, unless they are amplified by developmental studies." We believe that integumentary studies combined with those of histogenesis should be incorporated routinely into embryological studies, particularly those intended to have systematic application.

Many embryological studies are devoted to abnormal or exceptional cases, and there is less attention generally given to those characteristic features for particular groups that may have much greater taxonomic importance. In many references, it is difficult or impossible to determine which was the characteristic state for the taxon being investigated. Thus, the archesporium may be described as one- to three-celled or as one-celled but occasionally multi-celled, but without any explanation as to which was the characteristic state for that taxon. Exact statements about the proportions in which these different states were represented will be important for a proper evaluation of embryological reports and for promoting their utility in the future. Similar observations could be applied to reports of the characteristics of megaspore tetrads, functional megaspores, the number of nuclei in tapetal cells, and of microspore tetrads. Thus we would conclude that embryological studies should be more extensive in respect of the features that they consider and report, and more precise in terms of the way in which they handle anomalous or exceptional situations encountered.

In conclusion, embryological features afford a sound basis for the delineation of Myrtales. There are, however, many gaps to be filled in our knowledge of the taxa that clearly belong within this order, and other taxa that may or may not be directly related to it. A careful choice of the characters to be examined and critical descriptions of these characteristics will assist greatly in our ongoing evaluation of relationships within Myrtales and allied groups.

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